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SEGMENTATION OF THE OVUM, WITH ESPECIAL REFERENCE TO THE MAMMALIA.

BY CHARLES SEDGWICK MINOT.

(Concluded from page 481.)

DURING all these early stages the cells (segmentation spheres) are naked, *i.e.*, without any membrane; the nuclei, when not in karyokinetic stages, are large, clear, and vesicular; the yolk granules are small, highly refractile, and more or less nearly spherical; they show a marked tendency to lie in the cell half-way between the nuclear and the edge of the cell, or when the cells are large, around the nucleus and at a little distance from it.

It is at about this stage that the ovum passes from the Fallopian tube into the uterus, where it dilates into what is known as the *blastodermic vesicle.* This dilatation is due principally to the multiplication and flattening out of the cells of the outer layer, and of course involves the expansion and consequent thinning of the zona pellucida, (compare Figs. 8 and 13.) The inner mass meanwhile remains passively attached to one point on the circumference of the vesicle, (Fig. 11, *i.m.*) By this process the thin fissure between the inner mass and the outer layer becomes a considerable space, (Fig. 13).

The blastodermic vesicle continues to expand, and in the rabbit and mole there is a corresponding enlargement of the tubular uterus at the point where the vesicle is lodged. "It is clearly impossible for the delicate walled ovum to expand in the form of a vesicle, and distend the uterine walls by virtue of the growth of its cells; it must be therefore concluded that it obtains some support. This support is rendered from within. The vesicle contains a transparent fluid, the nature of which I am only sufficiently conversant with to say that, after a treatment with alcohol, a white precipitate is present in the vesicle. It is equally evident that this fluid can only have been obtained from the uterus, and that it is present within the vesicle at a very considerably greater pressure than in the uterus' itself. Such a condition is caused by means of the cells of the wall of the vesicle; this function being performed against a pressure which is greater on their inner than on their outer side, exactly as the cells of the salivary glands are known to act. The uterine fluid is secreted by glands present in great numbers in the uterine tissue, and is poured through their open mouths into the cavity of the uterus. There is every probability it has nutritive

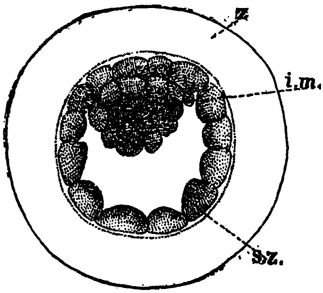

FIG. 11.

Young blastodermic vesicle of a mole, after Heape: *M*, mucous envelope; *z*, zona pellucida; *i m*, inner mass; *en*, entoderm; *s c*, segmentation cavity.

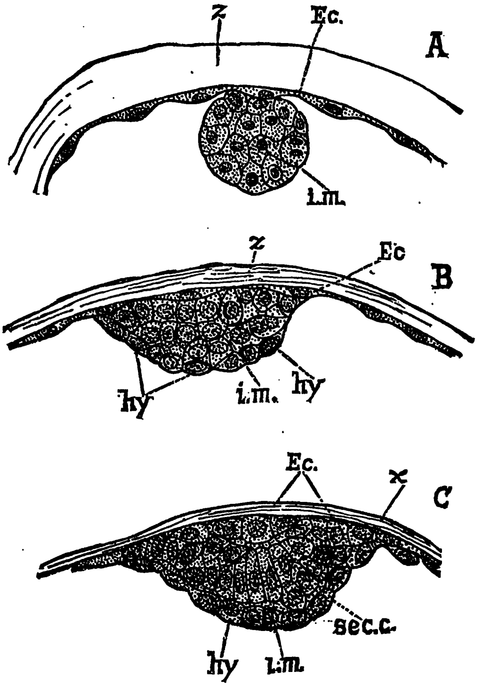

FIG. 12.

Sections through the inner mass of the blastodermic vesicle of the mole at three successive stages: *z*, zona pellucida; *s z* subzonal layer; *i m*, inner mass.

qualities, since it is thence taken up into the cavity of the embryonic vesicle, which eventually functions as a yolk-sac, in the walls of which embryonic blood-vessels ramify."—*Heape.*

The inner mass (Fig. 11, *i.m.*) does not at first grow much, and retains its rounded form, becoming, at least in the mole, nearly globular. (Fig. 12, A.) The inner mass subsequently flattens out, becoming lens-shaped, thinner, and of larger area. (Fig. 12, B.) It continues spreading laterally, and separates into three distinct layers. The ovum now consists of a very thin zona pellucida (Fig. 13, *z*), close against which is a single layer of thin epithelial cells, *En:* at one pole this layer is interrupted by a lens-shaped mass, *i.m.*, formed by three layers of cells. These three layers were first clearly described by E. van Beneden *9*, and have been since figured by him *10;* van Beneden identified these three layers with the three permanent germ-layers, which do not arise until later. Rauber, however, showed that both the

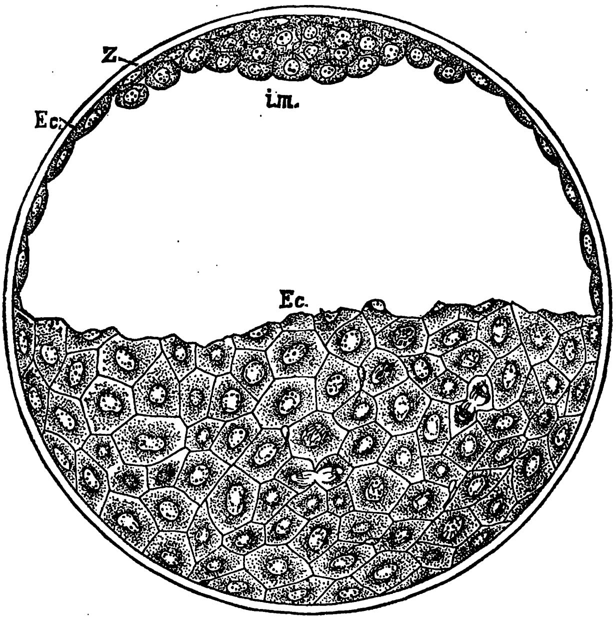

FIG. 13.
Ovum of rabbit ninety-four hours after coitus, after van Beneden: *en* subzonal epithelium (entoderm); *z*, zona pellucida; *i m*, inner mass of cells.

outer layers enter into the formation of the ectoderm, while the inner layer is concerned in the production of the permanent entoderm; the outermost layer Rauber terms the Deckschicht Lieberkühn *31a*, and others have since then confirmed Rauber's results.

Homologies of the mammalian blastodermic vesicle.—We have so little accurate information concerning the details of the formation of the blastodermic vesicle, that any interpretation must be tentative. I still consider, however, the view which I brought forward in 1885 (*Buck's Reference Hdbk. Med. Sciences*, I., 528), as the most satisfactory, and preferable to the similar explanation advanced independently and simultaneously by Haddon, *20*, and reproduced by him briefly in his "Practical Embryology," 47–48. F. Keibel, *27*, advocated similar interpretations two years later, but without quoting Minot or Haddon. I regard the subzonal epithelium as the entoderm, and the inner mass of cells as the primitive blastoderm or ectoderm: by so doing the parts can be readily and exactly homologized with the parts in the frog's ovum, as will be evident at once if the diagram (Fig. 14) of the mammalian vesicle be compared with the section of a segmented amphibian ovum, (Fig. 4).

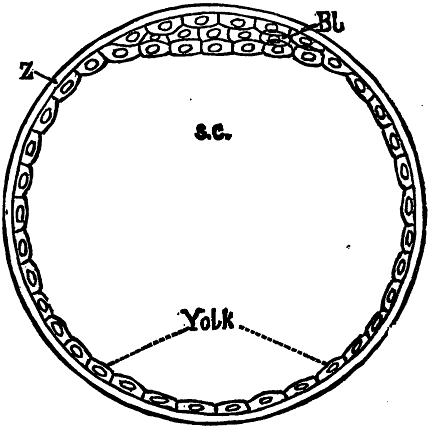

FIG. 14.

Diagram of a segmented mammalian ovum: *z*, zona pellucida; *Bl*, primitive blastoderm; *s c*, segmentation cavity; *yolk*, layer of cell representing the remnant of segmented yolk.

The primitive blastoderm *Bl.* or ectoderm consists of several layers of cells rich in protoplasm; below it is the large segmentation cavity, *s.c.*, relatively much larger in the mammalian than in the amphibian ovum. At its edge the primitive blastoderm joins the entoderm *yolk*, which in amphibia is a large mass, in mammals only a single layer of cells. Now, we know that the ancestors of the higher mammals had ova with a large amount of deutoplasm, which in the course of evolution has been lost, so that in the ova of the Placentalia there is very little yolk material. We know, further, that the readiness of cellular divisions depends on the amount of yolk; hence when the yolk is lost, we should expect to find the entoderm, which, as we have seen, is derived from the vegetative substance of the ovum, to be represented by relatively small cells. If we imagine the number of entodermic cells in the frog's ovum (Fig. 4, *Yolk*) reduced, their connection with the primitive blastoderm and their character as a continuous layer being preserved, we obtain at once the characteristic arrangement of the mammalian blastodermic vesicle, (Fig. 14.) The homology here established is further confirmed by the coarse net-work of protoplasm in the cells of the outer layer of the vesicle (Ed. van Beneden, *10*), suggesting at once the meshes which have been emptied of their deutoplasm. Adam Sedgwick, *43*, has shown that in the ova of *Peripatus capensis* the yolk matter has been lost, though abundant in other species of the same genus, and the coarseness of the protoplasmic net-work is preserved as evidence of the granules formerly present. This observation serves to confirm the view I have suggested as to the significance of the wide-meshed reticulum of the cells of the mammalian sub-zonal layer, (Fig. 14, *Yolk.*)

The disposition of the animal pole in the ovum before segmentation also conforms to the homologies here advocated. It will be remembered that the protoplasm of the animal pole extends far into the ovum, and is enveloped by a cup (deutoplasm zone) of the substance of the vegetable pole. Hence when the animal pole forms cells they lie as an inner mass, (Fig. 11, *i.m.*)

If Minot's view be adopted, then the ectoderm lies within the entoderm at a certain stage of development, for the one cell which retains, as shown in Fig. 8, the connection of the ectoderm with the exterior, is subsequently overgrown by the outer layer of cells (van Beneden, Heape). There is then a complete inversion of the germ layers in all (?) placental Mammalia. In most cases the inversion is temporary; the inner mass, as described above, flattens out, and probably flattens out *inside* the outer epithelial layer; if this is the case, then the external layer of the lens-shaped mass (Fig. 12, B and C, *im*) is really entoderm; this layer is Rauber's *Deckschicht*, which, as already stated, usually disappears, leaving the true inner mass, or permanent ectoderm, to form part of the surface of the blastodermic vesicle, so that, with the exception of the reduction in the dimension of the entoderm, the relations are the same as in other vertebrate ova.

The inner layer of the flattened inner mass gives rise to the entoderm, and this at first sight appears to be conclusive evidence against the homology here drawn between the inner mass and the primitive ectoderm of other vertebrates. The same thing was formerly supposed to occur in the blastoderm of other vertebrates, but it is now known that the entoderm is added from another source to the under side of the primitive blastoderm or ectoderm, and though we possess no exact information whatever as to the origin of the entodermic cells under the primitive blastoderm of the Mammalia there is no reason to assume that they arise in a manner fundamentally different from that typical of other vertebrates. We may therefore dismiss this objection. The origin of the entodermic cavity I hope to discuss on another occasion.

Planes of Division during Segmentation.—The plane of the first divisions determines those of the subsequent divisions, and also of all the axes of the embryo.[1] It is itself determined by the position of the long axis of the first amphiaster or nuclear spindle, to which it is at right angles. It, therefore, is a matter of great interest to ascertain what factors determine the position of the first spindle, or, in other words, the axis of elongation of the segmentation nucleus. So far as at present known there are two factors: I. Relation to the axis of the ovum; II. Position of the path taken by the male pronucleus to approach the female pronucleus. The axis of the ovum is fixed before impregnation. It passes through the center of the animal and that of the vegetable pole. Usually the nuclear spindle which leads to the for-

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[1] In certain cases, notably in birds as described above, the segmentation is irregular; and it is, therefore, not known yet whether the scheme of arrangement of the cleavage planes here given can be applied to all ova or not. We may say, however, that the scheme is the primitive one, from which any modifications arose phylogenetically. The best discussion is by A. Agassiz and Whitman, *1*, 34–41.

mation of the polar globules has its long axis coincident with that of the ovum, hence the point of exit of the polar globule marks one end of the ovic axis. *The first amphiaster or spindle is always at right angles to the ovic axis.* This, however, leaves the meridian plane undetermined. Roux, *39*, from a series of interesting experiments on frog's ova, concludes that the plane is fixed by the path of the spermatozoon. So far as I know this idea was first suggested by Selenka, in 1878, in his paper on "The Development of *Toxopneustus variegatus*." Compare also Mark, *32*, p. 500. In the frog's egg the path of the male pronucleus is marked by a line of pigment, as was first described by van Bambecke, *4*, p. 65, and has been well figured by O. Hertwig, *25a*, Pl. V., fig. 4. The pigment renders it easy to ascertain the position of the male road, even after the first cleavage of the ovum. This Roux has done in sectioned ova, and from experiments and observations reaches this result: *The long axis of the first segmentation spindle lies in a plane which passes through the axis of the ovum and the path of the male pronucleus.* If Roux's conclusion is confirmed, it will become of fundamental importance. Yet there must be other factors which can at least replace the male pronucleus in this special role, since the development of pathenogenetic ova, in which there is no male pronucleus at all, is equally determinate. It is probable that the distribution of the protoplasm is the real cause determining the position of the nucleus; thus in oval eggs the spindle lies in the direction of the long axis. It is quite probable that if the male pronucleus has the effect ascribed to it by Roux, it produces it indirectly by altering the distribution of the protoplasm within the ovum; that such alteration takes place is indicated by the occurrence of the male aster.

That the first cleavage plane is determined by relations existing in the unimpregnated ovum has been suggested by O. Schultze in consequence of his finding the germinal vesicle lying excentrically in the eggs of the brown frog. Schultze suggests that the first plane passes through the ovic axis and the excentric nucleus. Roux, Biol. Col., VII., 420, maintains that this suggestion is set aside by his own observations cited above. For further discussion see Schultze's short note, *42*, and Roux's rejoinder, *9*. I think the question whether the first cleavage plane is determined by the ovum's structure or not is still an open one.

As already stated, in the primitive segmentation, both invertebrate and vertebrate, the second cleavage plane is at right angles to the first, and also meriodional, while the third plane is at right angles to both the first and second, and therefore equatorial. In some meroblastic vertebrate ova this regularity is entirely lost.

Differentiation of the ectoderm and entoderm.—As already pointed out the essential feature of segmentation is the unlikeness of the cells produced; the manifold variations in the process of segmentation depend chiefly on the amount of yolk.

Minot, in 1877, *33*, first established the generalization that *in all animals the ovum undergoes a total segmentation during which the cells of the ectoderm divide faster and become smaller than the cells of the entoderm.* Compare Fig. 15. There are, however, a small and, I think, diminishing number of cases, where the process of segmentation is imperfectly understood, and which cannot yet be shown to conform to this generalization. "All the known variations in the process of segmentation depend merely upon: 1. The degree of difference in size between the two sets of cells; 2. the time when the difference appears; 3. the mode of development, whether polar or by delamination,[2] either of which may or may not be accompanied by axial infolding. In gastropods, planarians, calcispongæ, gephyrea, annelida, fish, birds, and arthropods the difference is great and appears early. In echinoderms, most

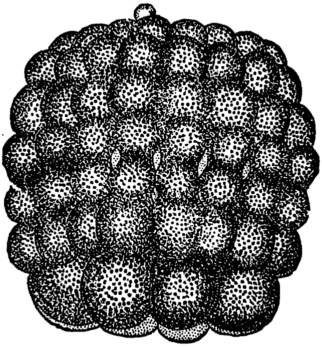

FIG. 15.

Ovum of *Amphioxus lanceolatus* during segmentation; stage with 88 cells, x 280 diams., after B. Hatschek. One pole is occupied by large entodermal, the other by smaller ectodermal cells.

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[2] There is not a single satisfactory description known to me of the process of the so-called delamination and I feel a very great skepticism as to its being an actual occurrence. It is certainly at most a very rare and probably secondary modification of segmentation. It does not occur among vertebrates.

cœlenterates, some sponges, in nematodes, amphibians, etc., it is less marked and appears later.

In most cases the entodermic cells are very decidedly larger and less numerous than those of the ectoderm. This distinction is obviously necessary on account of the mutual relations of the two primitive layers. The ectoderm has to grow around the entoderm, which it can do only by acquiring a greater superficial extension; this the ectoderm accomplishes by dividing very quickly at first into small cells. After the entoderm is fully enveloped it may then continue to grow until its superficies is much greater than that of the outer layer, within which, however, it still finds room by forming numerous folds; thus is gradually reached the condition in the higher adult animals, where the intestine sometimes has an enormous surface, but is, nevertheless, contained in body-walls covered by ectoderm presenting much less surface. It is, therefore, only during the early stages of segmentation that we find the entoderm expanding more slowly than the ectoderm.

The terms *holoblastic* and *meroblastic* are applied to ova according to their manner of segmentation. The first is employed for those ova in which there is either very little or only a moderate amount of yolk, so that the whole of the ovum splits up into distinct masses (cells) which enter into the composition of the embryo. The second designates ova with a very large amount of yolk, so that while the protoplasm from which the ectoderm arises divides rapidly into distinct cells, the entodermal portion merely develops nuclei at first, with the result that while one portion of the egg is "segmenting," another portion (the entodermal) remains unsegmented, so far as the external appearances are concerned. Eggs, then, with much yolk undergo the so-called partial segmentation; hence the adjective *meroblastic*.

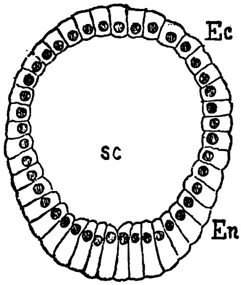

FIG. 16.
Blastula stage in the development of *Echinocardium cordatum*, after Selenka.

Whatever the exact mode of segmentation, there results always the same type of organization, to which Minot has applied the term *diaderm ;* it is characterized by consisting of two plates of cells, differing in character, joined at their edges (ectenal line), and surrounding a central segmentation cavity: the two plates or laminæ are the two primitive germ-layers, the ectoderm and entoderm. The earliest form of the diaderm is that known as the *blastula*, as Haeckel has felicitously named the first larval form of the lower animals. In the blastula we have a simple epithelial vesicle, the cavity of which is the large segmentation cavity (Fig. 16); the epithelial layer is one cell thick and divided into two regions, the one composed of smaller cells is the ectoderm, *Ec*, and the other, of larger cells, is the entoderm, *en*. This stage occurs with sundry modifications in a great many invertebrates. These modifications are due principally to the increase in the size of the entodermic cells, which, as already pointed out, results from the increase of the yolk matter in the ovum. Thus in many mollusks the entodermic cells are very large, and at first, few in number, (Fig. 17). By a still further modification the cellular yolk is replaced by a mass rich in deutoplasm, but not divided by cells, while at the same time the segmentation cavity is reduced by the invasion of the yolk mass. This is well exemplified in the ova of many arthropods, (Fig. 18). We have in this case the blastula type still evident, although the entoderm has at this stage no trace of its epithelial structure. In vertebrates we have the additional modification that cells are several layers deep in the ectoderm, and primitively in the entoderm also,—compare the section of the frog's ovum (Fig. 4). In certain forms, as we have seen, the entoderm is not

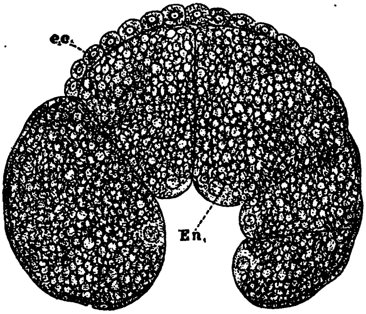

FIG. 17.
Blastula stage in the development of Natica; after Bobretzky.

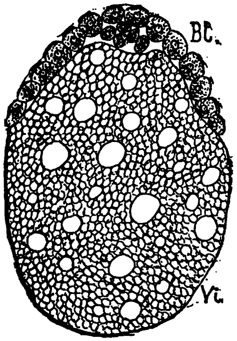

FIG. 18.
Section of the ovum of *Oniscus murarius ;* after Bobretzky. *Bl*, blastoderm: *Vi*, vitellus or yolk representing the entoderm.

divided into discrete cells, but remains one mass; this is the case in elasmobranchs and the amniota, but in the highest amniota (Placentalia) the yolk is lost and the entoderm is again represented by a single layer of cells (Fig. 13).

It seems to me evident that *the first step of development in the segmenting ovum is the differentiation of the two germ-layers, ectoderm and entoderm, resulting in the diaderm stage.* Diaderm is a term preferable to blastula, because the latter is applicable strictly only to a special larval form, while the former is a general term which refers to the essential differentiation at this stage. It is important to remark that the two layers are distinct in the diaderm or blastula stage; it is often erroneously affirmed that the blastula consists of a *uniform* layer of cells, part of which subsequently becomes the entoderm.

The segmentation cavity comprises the whole space between the entoderm and ectoderm; it is very early invaded by cells produced from the two primitive germ-layers. These cells are in vertebrates of many kinds, and enter the segmentation cavity at various periods. It is customary to group the cells which enter early into this cavity under the common name of *mesoderm,* and to consider them as a third and distinct germ-layer. For convenience we may adopt this custom, for, to a certain extent, the mesoderm of authors is a separate germ-layer, but it by no means includes all the tissues which occupy the space between the two primitive germ-layers. As the space between the entoderm and ectoderm is always homologous with itself it follows that the entire room between the epithelium (entoderm) of the digestive tract and its appendages on the one side, and the epiderm on the other, is homologous with the segmentation cavity.

The mesoderm of authors comprises three tissues: (1), free wandering cells (*mesamœboids*); (2), embryonic connective tissue or cells connected together by processes (*mesenchyms*); (3), epithelium, which forms two or more separate sacks. The origin of the mesoderm and the relations of the three tissues it contains do not fall within the scope of this article.

The Gastrula theory.—In invertebrates with holoblastic ova the blastula passes into a stage known as the *Gastrula.* Gastrula is, properly speaking, a new name for a larval form called *Planula* by older writers; but the term is now generally employed to designate an ideal embryonic stage supposed to be common to all multicellular animals.

The blastula changes into a gastrula by a process of invagination. The entodermal area of the blastula flattens out, the ectoderm meanwhile expanding by multiplication of its cells; after flattening, the entoderm turns inward, forming at first a shallow cup, then a pit which has an opening or mouth, the rim of which is the ectental line. The larva is now a double sack, and has an external wall or ectoderm, and an internal wall or entoderm; the entodermic cavity is entirely distinct from the segmentation cavity. The process of gastrulation is here described as it occurs among the lower invertebrates.

Typical gastrulæ are the free swimming larvæ of many marine invertebrates. We may take as an example that of a sea-urchin, (Fig. 19). The larva is round; at one pole it has an opening, *M*, the gastrula mouth leading into an internal cavity; as this is a free swimming larva it is provided with long cilia for organs of locomotion; the cilia in many gastrulas are distributed over limited areas or they may be wanting altogether. The larva consists of a double sack,—a larger outer one of small epithelial cells, *ec*, the ectoderm; and a much smaller inner sack composed of larger entodermal epithelial cells, *en;* at the mouth, *M*, of the inner sack the two layers are continuous with one another; in the space between the two sacks, which corresponds to the segmentation

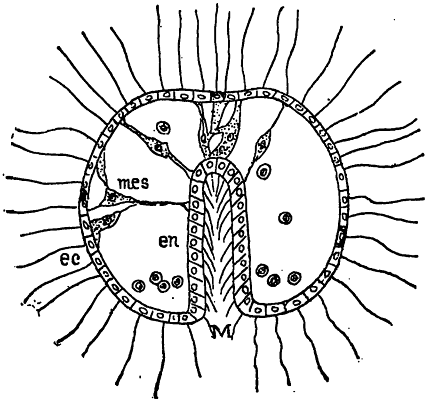

FIG. 19.

Section of a gastrula of *Toxopneustus lividus*, after Selenka; *ec*, ectoderm; *en*, entoderm; *mes*, mesoderm; *M*, mouth.

cavity, are a few scattered cells, the first members of the mesoderm, *mes.*

The entodermal sack of the gastrula is known as the *archenteron;* other terms are also in use, *e.g.*, mid-gut, cœlenteron, Urdarm, etc. The opening is known as the *gastrula mouth* (archistome, Urmund, etc.). The cœlenterates preserve the gastrula organization throughout life, but in all higher classes the archenteron gives rise, not only to the permanent digestive tract, but also to many appendages and derivatives thereof; and moreover the gastrula mouth closes over, and in vertebrates the true mouth is an entirely new formation which arises without any connection whatsoever, so far as known, with the gastrula mouth. By gastrulation the ectental line becomes the rim of the gastrula mouth.

A line passing through the centre of the mouth and the opposite pole of the gastrula is the so-called axis. Now if the mouth be elongated, there would at once be a new *longitudinal axis* marked out, and the gastrula would become *bilaterally symmetrical.* If, further, the mouth is pulled out into a slit, and in the process of evolution the lips come together and unite in their middle part, the animal would still have the two ends of the original mouth left open, and would so acquire two apertures to its archenteron, one anterior to serve as mouth, and one posterior to serve as anus. This hypothesis of the conversion of a gastrula into a bi-laterally symmetrical animal by the elongation of the mouth and concrescence of the lips or ectental line, was first suggested, so far as I am aware, by Rabl, *36.* A very perfect exemplification of the process is afforded by the developing ova of *Peripatus capensis* as shown by Balfour, *3*, and Sedgwick, *43*, Pl. XXXII. Figs. 23–26. There are, however, serious difficulties in applying the theory to bilateral invertebrates. I am strongly inclined to think that further research will obviate these difficulties.

In certain vertebrates and annelids the concrescence of the ectental line has been clearly demonstrated, but the process is rendered by secondary modifications much more complex than that described in the preceding paragraph.

The Gastrula theory is that all metazoa have a common inherited stage of development, which follows immediately after the diaderm; this stage is characterized by there being an outer ectodermal sack with a perforation, to the edge of which is attached the entoderm, which forms a closed inner sack, the archenteron.

The term gastrula was introduced by Haeckel, and is now universally used by embryologists. The discovery of the importance of the gastrula is due to the brilliant researches of Kowalewski on various invertebrates, including Amphioxus, then supposed to be a vertebrate. Haeckel then seized upon the idea of the gastrula, and wrote an essay, *21*, upon it, which from its brilliant style attracted much notice, and did much to direct attention to the important discovery of Kowalewski. Although Haeckel indulged his fantasy unduly, and was misled into speculations which are now unheeded and almost forgotten, he did great good by starting the interest of zoölogists in the right direction. By a remarkable coincidence Lankester published an essay, *31*, of a purport very similar to Haeckel's, at about the same time. A great deal remains to be done before the gastrula theory of evolution can be fully established, for there are many facts not brought into accord with the theory in its present form.

The gastrula, like the diaderm, varies greatly, the chief modifications depending on the amount of yolk present; this is illustrated by the accompanying diagrams, (Fig. 20). The mesoderm is intentionally omitted; A corresponds to such a larva as Fig. 19; the difference in size between the two sets of cells is slight but evident. In B the difference is more marked, and fairly represents a gastrula of Amphioxus. In C the difference is very great, and corresponds to that observed in certain gastropod larvæ. In

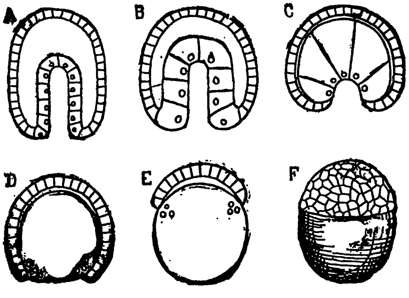

FIG. 20.

Diagrams of the principal modifications of the gastrula (see text), *A E* represent sections.

D the inner set is no longer separated into distinct cells, although there are a number of nuclei, each of which marks the centre of a future cell; in such instances we must regard the whole inner portion as not yet transformed into a definite entodermic *cell-layer*. This figure is particularly instructive, because it shows that what we call the yolk is not something distinct from the germ, but really belongs to the inner layer of the embryo. E shows a similar egg, in which the outer set of cells has not yet grown around the yolk. F shows the same egg, not in section but seen from the outer surface.

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